THE INHERITANCE OF PHOTOPERIODISM IN SNAP BEAN

(PHASEOLUS VULGARIS)

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ABSTRACT

The heredity of photoperiodic response of flowering in Phaseolus vulgaris was studied. The parents were classified into three types according to their photoperiod sensitivity--day-neutral (flower at any daylength), intermediate (require a night longer than 11.5 hours), and sensitive (require a night longer than 12 hours). Crosses between parents of the same phenotype generally produced F_1 and F_2 progenies which showed no segregation. The segregation patterns for photoperiodic response were determined for larger numbers of individuals by planting during the summer when days are too long for floral induction and assuming that each plant begins to flower when the daylength has shortened to the critical length required by that plant. Temperatures within the range experienced in the field were found to have an insignificant effect.

It is postulated that the inheritance of the photoperiodic response in these lines is determined by at least four major gene loci with dominance, epistasis, and independent segregation. A dominant N gene is postulated that permits flowering at any daylength. If the recessive n gene or a dominant inhibitor of the N gene, I_N, are present, there is an intermediate daylength requirement for flowering. A dominant Q gene which intensifies the short daylength requirement is also postulated. If the recessive q gene or a dominant inhibitor of the Q gene, I_Q, are present, the daylength requirement again is of the intermediate type. The day-neutral and intermediate parents therefore differ by two genes (at the N and I_N loci), and the intermediate and sensitive

parents differ by another two genes (at the Q and I_Q loci), so that the day-neutral and sensitive parents differ by a total of four genes. It is likely that additional genes with smaller effects may also be involved.

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INTRODUCTION

Daylength is important for determining the onset of flowering and seed production in many plants. Garner and Allard (1920) were first to report the flowering response of plants in relation to the relative daylength and gave the term 'photoperiodism' to this response.

Some plants have an absolute requirement for short or long days, whereas in others flowering may merely be promoted or inhibited. A few species flower only in intermediate daylength. Daylength is perhaps the most reliable and regular signal which controls flowering in plants.

Generally, short day plants inhabit tropical and subtropical areas, long day plants inhabit higher latitudes, and day-neutral plants are found in all areas. The critical daylength of strains within a species may vary considerably with the latitude at which the strain is growing. Knowledge of the genetic mechanism controlling photoperiodism would therefore be very useful when starting a breeding program in order to adapt a species to a particular photoperiod or to develop day-neutral cultivars.

The United States Department of Agriculture has introduced many lines of Phaseolus vulgaris from foreign sources, particularly from Central America, the generally accepted center of origin. Foreign sources of disease resistance especially are in use in all major breeding programs (Peterson, 1975). Many lines from tropical areas flower only under short day conditions and thus can not be matured outdoors in higher latitudes. Lines such as these often contain

genetic characters which may be useful in breeding programs. However, their short day sensitivity precludes their use in temperate zones as commercial cultivars, so their characters must be incorporated into adapted genetic backgrounds to be useful.

Some genetic studies regarding photoperiodism in beans have been carried out previously in temperate regions, but little information has been published for tropical lines. Therefore, the present study will attempt to determine the nature of inheritance of the high degree of daylength sensitivity found in some tropical lines (Hartmann, 1969).

LITERATURE REVIEW

The onset of flowering in response to daylength is an important factor limiting particular strains of crops to particular latitudes or seasons (Garner and Allard, 1920). According to Garner and Allard (1920, 1923) plants respond to photoperiods in three general ways:

1. Short day plants (SDP) flower in early spring or fall in temperate climates or in winter in tropical or subtropical climates. They must have a dark period longer than a critical length in each 24 hour cycle.
2. Long day plants (LDP) which flower chiefly in the summer in temperate climates will flower only if the light period is longer than a critical length in each 24 hour cycle. They flower with short dark periods.
3. Day neutral plants (DNP) flower irrespective of the photoperiod condition.

The sensitivity of the response varies with different species. Some may require only a single exposure to the inductive cycle while others may require several weeks of exposure. Also, a single species may include varieties with completely opposite types of photoperiodic responses.

The characteristic feature of photoperiodism is the biological measurement of the relative lengths of day and night (Salisbury and Ross, 1969). There are many experiments conducted on different aspects of photoperiodism in flowering. The literature is vast and

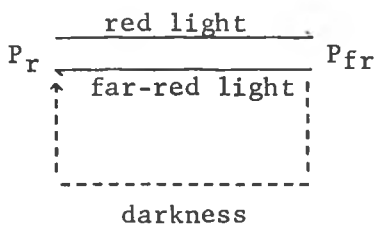
complex. The present review will consider general ideas of the photoperiodic mechanism in relation to flower induction.

Physiology of photoperiodism

The leaf is the locus of photoperiodic reception that influences the bud some distance away (Chailakhyan, 1969; Evans, 1971; Murneek, 1948; Salisbury and Ross, 1969; Vince-Prue, 1975).

The first step is photoperiodic induction which includes processes, under photoperiodic control, that occur in the leaf and lead to the production of floral stimulus (Evans, 1971; Vince-Prue, 1975). This is followed by floral evocation (Evans, 1971) which include processes that occur at the shoot apex in response to the arrival of the floral stimulus.

The plant's photoperiodic reception is spectrally discriminating and the photoreceptor pigment is phytochrome. There are two portions to the phytochrome molecule: a light absorbing portion (chromophore) and a large protein portion. Phytochrome exists in two mutually photoreversible forms: P_r and P_{fr}.



P_r, absorbing red light (665 nm), is converted to P_{fr}. P_{fr} absorbs far-red (725 nm) light, which converts it back to P_r. The P_{fr} to P_r conversion also takes place in the dark. P_{fr} may control the relative flow of substrate into several linked and competing synthetic pathways.

Some must operate only when P_{fr} is low or perhaps absent. Substrate level also apparently affects the relative flow into the competing pathways (Evans, 1971).

During the daylight period, P_{fr} is predominant in the leaf. On transfer to darkness, the equilibrium is displaced in the direction of P_r, and, after some time, the P_{fr} level falls to a threshold value. In SDP, the P_{fr} must be absent or remain below the threshold level for a duration long enough to allow floral hormone production. The flowering response thus depends on the duration of dark period. In LDP, however, it is assumed either that a dark inhibitory process begins when the P_{fr} level falls to a threshold value, or that floral hormone production continues only when P_{fr} is present over a long period of time.

The mechanism of phytochrome activity in regulating the production of floral stimulus is not known. However, there are a number of hypotheses about the mechanism of phytochrome action. It is suggested that the phototransformation of phytochrome may very rapidly lead to an alteration of cell membrane permeability (Briggs and Rice, 1972). Such a change might control various processes leading to flowering by controlling the passage of substances into or out of cellular compartments.

An alternative hypothesis proposes that phytochrome interacts with the genome and affects differentiation by the induction or repression of enzyme formation (Mohr, 1966). The phytochrome molecule may act as an enzyme. When light is absorbed by the pigment, the light energy changes the structure of the enzyme portion, rendering the enzyme active.

Whether phytochrome acts enzymatically or on membrane properties, it is likely that both P_{fr} and substrate have to be available in sufficient amount for several linked pathways leading to synthesis of floral stimulus to occur.

Following induction in the leaf, the floral stimulus is translocated to the shoot apex where floral evocation occurs. The arrival of the floral stimulus at the apex leads to RNA synthesis and an increase in protein level (Salisbury and Ross, 1969; Evans, 1971). An increase in DNA levels also occurs early. A sharp increase in the mitotic index precedes and accompanies the morphological changes associated with the initiation of floral primordia and their subsequent development. A threshold level of floral stimulus is necessary for flowering. Differences in photoperiodic sensitivity can be attributed to differences in sensitivity of the shoot apices to the floral stimulus (Vince-Prue, 1975). The floral stimulus may act at the transcriptional level by specifically releasing repressed floral genes. This will lead to the production of new messenger RNAs and enzymes required for the initiation and the development of the floral primordia. The floral stimulus may also act at another level such as translation (Vince-Prue, 1975).

Temperature effects

The response of a given plant to daylength may be profoundly modified by environmental factors, especially temperature. Plants in which flowering response is wholly independent of temperature are rare. Much of the uncertainty as to the proper photoperiodic classification

of some plants has been due to the temperature effect (Salisbury and Ross, 1969). The modifying effects of temperature on photoperiodism have been known ever since the observations of Garner and Allard (1920) and have been confirmed by many other workers (Coyne, 1966; Johnson et al., 1960; Major et al., 1975; Murneek, 1948; Quinby, 1973; Roberts and Struckmeyer, 1939).

Temperature affects the time of floral initiation differently in different cultivars. Plants may respond like one response-type at one temperature regime but not at another. There are a number of species which are strongly photoperiodic only within a particular temperature range (Cathey, 1954; Roberts and Struckmeyer, 1939). Outside this range some cultivars may fail to flower entirely or flowering may be very much delayed. For some plants temperatures may partially or wholly substitute for photoperiod treatments, or vice-versa (Salisbury and Ross, 1969; Vince-Prue, 1975).

In general, an increase in temperature, within favorable limits, increases the rate of plant growth and development. In some way, temperature influences the synthesis of the floral stimulus or its accumulation at the shoot apex (Quinby, 1973). With increasing latitude the relationship between the promoting action of the day-length and the inhibiting action of low temperature becomes critical for late maturing varieties (Garner and Allard, 1920). The cooler temperatures and longer photoperiods encountered at more northerly latitudes were found to be additive in their delaying effect on flower in SD soybean (Johnson et al., 1960). The delaying effect of cool

spring temperature on flowering predominated in the early part of the growing season whereas the long daylength effect predominated and delayed flowering during the summer.

It has been suggested that in sorghum the alleles at the maturity loci respond differently to temperature (Quinby, 1973). It has also been proposed that certain genes concerned with the temperature response affect the expression of the genes for photoperiodic response in rice (Sampath and Seshu, 1961). The interaction of the temperature and photoperiodic responses is the probable cause of differences in flowering-time from year to year in strongly photoperiodic species (Vince-Prue, 1975).

Genetics of photoperiodism

A fair amount of knowledge is known about the inheritance of photoperiodic response (Skripchinskii, 1971). Many different patterns of the genetics of photoperiodism have been reported (Allard, 1919; Barber, 1958; Chandraratna, 1955; Chang et al., 1969; Coyne, 1966; Goodwin, 1944; Klaimi and Qualset, 1973; Padda, 1971; Povilaitis, 1971; Sen et al., 1964; Verma, 1971). Skripchinskii (1971) stated that all known genetic mechanisms may play some role in determining the photoperiodic response in some plants.

Allard (1919) studied the inheritance of photoperiodic response in a cross between a short day tobacco variety and a day-neutral one. The F_2 segregated in the Mendelian ratio of 3 day-neutral to 1 short day. He thus reported that one allelic gene pair was involved, with the short day response being recessive. Povilaitis (1971) also found

that the short-day response was recessive to the day-neutral response in tobacco.

Chandraratna (1955) studied a range of rice material and observed dominance of the short-day response in the F_1 and monohybrid segregation in the F_2. Later, Sen et al. (1964) confirmed that photoperiod sensitivity in rice is governed by a single gene pair. However, a continuous range of flowering within the sensitive and insensitive groups also indicates the presence of modifiers in this species. Lin (1972), working with a cross between weakly short-day sensitive and insensitive rice, found multiple factor inheritance and partial dominance of sensitivity over insensitivity.

Sen and Ghosh (1961) reported that in green gram, short-day sensitivity was controlled by one recessive gene. One or more systems of genes modify the action of the major gene.

Barber (1958) found complex genetic mechanisms determining photoperiodic response in pea. In crosses between long-day and day-neutral pea varieties, the F_2 showed monogenic segregation with the long-day response dominant. In addition to the major gene, there are two other gene systems controlling flowering: a system of modifier genes and a system of polygenes.

Klaimi and Qualset (1973) studied the inheritance of photoperiodic response in crosses involving spring wheat and winter wheat cultivars. The results were explained on the basis of two major gene loci with three alleles at each locus. Genes with minor effect also affected the photoperiodic response in a quantitative manner.

Sorghum cultivars grown in the United States can be classified as early, intermediate, or late. Quinby (1973) reported that four gene loci control time of floral initiation and duration of growth.

Goodwin (1944) studied three strains of seaside goldenrod and indicated the minimum number of genes controlling the photoperiod requirement might be as many as nine. It is probable that these genes are located in many of the linkage groups.

In spite of the great diversity of genetic control of response to photoperiod, it has been assumed that a single basic mechanism which is dependent on light absorbed by phytochrome controls the photoperiodic response in all plants (Vince-Prue, 1975). The different patterns of genetic control suggest that the same overt behavior may have evolved along different evolutionary pathways.

Studies on photoperiodism in beans

Phaseolus vulgaris is the best known and most cultivated species of Phaseolus (Gentry, 1969; Purseglove, 1968). The cultivated types differ greatly from their wild ancestors. Cultivated types are relatively shorter-lived annuals with larger, fleshier pods, and seeds which are generally larger and more permeable to water.

Cultivars are grown for their immature edible pods (snap beans), for the dry ripe seeds (field beans), and to a lesser extent for green-shelled beans which are canned or frozen. In the United States the common bean is ranked fourth among the frozen vegetables (Purseglove, 1968). Fresh beans are on the market every month of the year, being produced in the southern states in the winter, the northern

states in the summer, and in the intermediate states in the spring and fall.

P. vulgaris is self-fertilized, pollination taking place at the time the flower opens. Selections are easily made with seeds from individual plants and pure lines can be soon established.

Improved cultivars are constantly being produced in temperate countries, attention being paid to yield, improved habit, time to maturity, disease resistance, etc. Little work has been done on improvement in the tropics.

Bean cultivars show different responses to photoperiod. Garner and Allard (1923) noted that some varieties of P. vulgaris were photoperiodically sensitive. Later, Allard and Zaumeyer (1944) tested 79 lines and reported all the bush-type beans were day-neutral, while the semi-pole and pole types were either photoperiodically sensitive or day-neutral. Cultivars adapted to the temperate zone have been found to be either day-neutral or of a short-day type of a quantitative nature in which flowering was delayed under increased lengths of photoperiods (Coyne, 1966, 1967, 1970; Ojehomon et al., 1968; Padda and Munger, 1969; Zehni et al., 1970). In lines introduced from the tropics there have also been reported short-day types with a qualitative daylength requirement (Garner and Allard, 1923; Hartmann, 1969).

It has been found that some cultivars develop normally in short days (11 hours) but growing the plants in a 15 hour daylength results in abscission of the flower buds, although the rate of floral initiation is unaffected (Ojehomon et al., 1968, 1973). Zehni et al. (1970)

studied the role of the first trifoliate leaf in perceiving and transmitting both long and short-day stimuli. Evidence was found that a transmissible inhibiting substance was formed during long days and a promoting substance was formed during short days. Bentley and his co-workers (1975) studied the effects of photoperiod on endogenous concentrations of abscisic acid (ABA). They found that under long days, there was a greater production of ABA in the leaves and an increased accumulation of the substance in the bud, leading eventually to their inhibition and abscission. They also suggested that cytokinin might be the promotory substance.

Much genetic work on photoperiodism has been done by Coyne and his co-workers in Nebraska (Coyne and Mattson, 1964; Coyne, 1966, 1967, 1970; Coyne and Schuster, 1974; Coyne et al., 1973). Their main objective has been to develop early maturing, dry bean cultivars tolerant to bacterial pathogens. They found that tolerance to the bacterial pathogens was often associated with delayed flowering. They found that delayed flowering was due to an interaction between high temperature and long photoperiod and under the control of relatively few genes.

The inheritance of this flowering response was conditioned by both dominant and recessive genes (Coyne and Mattson, 1964). The F_2's segregated into digenic ratios of 9:7 and 15:1. Using different day-neutral varieties, Coyne (1966) reported quantitative inheritance in which the F_2 population showed a continuous and unimodal distribution. However, the same population grown in a different season in a later

study (Coyne, 1967) produced a bimodal 9:7 distribution. Coyne concluded that in the original test, the temperature was not high enough to delay the flowering of the short-day progeny. Thus, a continuous distribution was observed in the segregating generation and the major gene effects were not expressed.

Monogenic inheritance has also been reported, with the short-day response controlled by a single major dominant gene (Coyne, 1970). Padda and Munger (1969) found that the flowering response was controlled by two major genes whose action was dependent on temperature. Under long photoperiods (16 or 18 hours), the dominant allele of one gene caused delayed flowering under high temperature while the dominant allele of the other gene caused delayed flowering under low temperature. However, under short days (8-12 hours) these cultivars flowered normally.

MATERIALS AND METHODS

Parental lines

Eleven Phaseolus vulgaris lines of different photoperiodic responses were selected for this study (Table 1). Two cultivars, OSU 949-1864 and Harvester, have been reported to be day-neutral (Coyne, 1966). The seeds of OSU were obtained from Dr. W. A. Frazier at Oregon State University. Seeds of Harvester were obtained from a commercial source.

Also selected were nine tropical plant introduction (PI) lines which have been reported to not flower until days shorten in the fall (Hartmann, 1969). These PI lines were obtained from the Regional Plant Introduction Station at Pullman, Washington.

All parental lines were uniform pure lines and have shown no segregation.

Calculation of daylength

The light intensity at sunset, on a clear day, measured perpendicular to the sun's rays, was about 35 foot-candles and the intensity decreased to 10 foot-candles in 7 minutes (Table 2). The time from sunrise to sunset was thus used as the effective daylength and was obtained from the American Nautical Almanac (1974) for Hawaii latitude (21 N). The longest days in the year, 13.4 hours, occur from about June 15 to June 30. After July 1, the daylength gradually decreases, finally reaching a minimum level of 10.8 hours from about December 15 to December 30. Daylength variation during the year is presented in Fig. 1.

Table 1. Parental lines of Phaseolus vulgaris

	Abbreviation	Growth habit	Origin	Flower color	Daylength (hr.) at which short-day lines bloomed[a]
Blue Lake derived OSU 949-1864	OSU	determinate	U.S.A.	white	
Harvester	HAR	determinate	U.S.A.	white	
PI 291002	002	indeterminate	Peru	purple-red	11.8
PI 291005	005	indeterminate	Peru	white	12.5
PI 291006	006	indeterminate	Peru	pink	11.5
PI 290999	999	indeterminate	Peru	lavender	12.0
PI 202081	081	indeterminate	Mexico	purple	12.0
PI 202831	831	indeterminate	Mexico	purple	12.3
PI 203914	914	indeterminate	Mexico	white	12.0
PI 203916	916	indeterminate	Mexico	white	11.8
PI 203924	924	indeterminate	Mexico	purple	12.0

[a]As reported by Hartmann (1969).

Table 2. Light intensity at sunset on the campus of the University of Hawaii, Manoa

September 14 (sunset 6:36 p.m.)		October 15 (sunset 6:07 p.m.)	
Time	Intensity (f.c)	Time	Intensity (f.c.)
6:36 p.m.	34	5:22 p.m.	4800
		5:25	3400
6:40	18	5:37	3200
		5:41	2800
6:42	12	5:45	2000
		5:49	1400
6:43	10	5:53	400
		5:54	260
6:44	8	5:55	240
		5:56	220
6:46	5	5:57	180
		5:58	150
6:47	4	5:59	120
		6:00	100
6:50	1	6:01	80
		6:03	66
		6:05	56
		6:07	36
		6:08	30
		6:09	26
		6:10	22
		6:12	16
		6:14	10
		6:15	8
		6:16	6
		6:17	5
		6:19	2

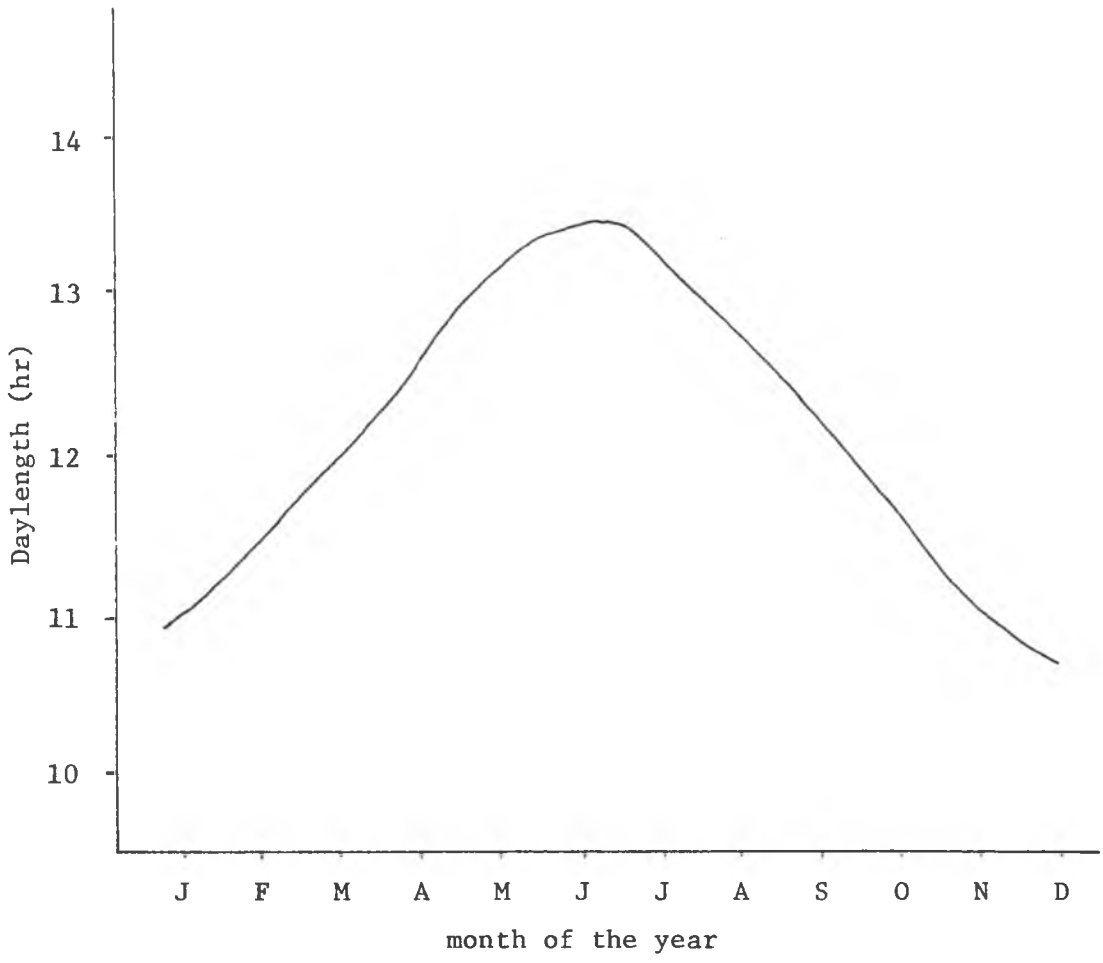


Fig. 1. Daylength (sunrise to sunset) variation during the year at Honolulu (Lat. 21 N).

Greenhouse cultural conditions

The seeds were planted in a mixture of equal parts by volume of soil, vermiculite, and wood shavings in 20 cm plastic pots. Five grams of a complete fertilizer (10-10-10) were added to each pot 1 and 3 weeks after planting. The pots were placed randomly on the benches. Plants were watered once a day and were sprayed weekly with insecticide, alternating Diazinon and Cygon, for the duration of the experiment. The temperatures in the greenhouse varied from 30 $\pm$ 5 C day and 21 $\pm$ 3 C night during the summer (May to September) to 25 $\pm$ 5 C day and 18 $\pm$ 3 C night during the winter (November to March). The relative humidities during the summer were 57 $\pm$ 20 % day, 90 $\pm$ 10 % night, and during the winter were 65 $\pm$ 20 % day and 90 $\pm$ 10 % night.

Photoperiodic response of parental lines - greenhouse

To determine the flowering response of the parental lines under natural daylength, plantings were made on six different dates throughout the year. Four seeds of each line were planted in each of two pots in every planting. Flowering was recorded for each plant as the day on which the first flower opened.

To determine the flowering response under controlled daylength, plants from all parental lines were exposed to different daylengths in the greenhouse. Ten pots with four seeds each were planted for each parental line. Beginning 5 days after planting all plants were exposed to a 15-hour daylength for 11 days. This was to insure against accidental induction of flowering by natural daylength. Sixteen days after planting, the pots were moved to benches that could be covered

by black plastic to create specific daylengths. Five different daylength treatments were used: 8, 10, 12, 14 and 16 hours. Two pots of plants from each parental line were exposed to each treatment.

All treatments received 8 hours of natural daylength per day. Then they were covered with black plastic, and additional daylength was provided by 60 watt incandescent light bulbs suspended 2 m above the pots. The light was controlled by electronic timers to insure accuracy of the photoperiods. The plastic covers were removed manually in the morning. The maximum temperature increase measured under the plastic enclosure was 3.5 C. The plants were allowed to grow under the controlled photoperiods for 50 days.

Growth chamber study

A study was carried out to determine the effects of temperature on floral initiation and development.

Uniform seeds of line 924, which flowers under photoperiods of 12 hours and less, were sown in 20 cm pots containing a mixture of equal parts by volume of soil, vermiculite, and wood shavings on February 8, 1975. They germinated in the greenhouse at a temperature of approximately 29.5 C day and 24 C night. Five days after planting, the plants were exposed to a 15-hour photoperiod for 11 days. Daylight was supplemented with incandescent light. This was to insure against floral induction by natural daylength before the plants were transferred to the growth chamber with different temperatures. A 10-hour photoperiod was produced in each growth chamber by a combination of incandescent and fluorescent bulbs, with an intensity of 2500

foot-candles at 30 cm above the pots. Two temperature treatments, 30 C day/24.4 C night and 24.4 C day/16.7 C night were chosen to simulate the average summer and winter temperature conditions in Hawaii. Other conditions were the same for both treatments. Because of the limited space in the growth chamber, nine pots with four or five plants each were used. The plants were kept under temperature treatments for 28 days.

Four complete plants were harvested randomly from those grown at both temperature regimes at 3-day intervals to examine the buds under a dissecting microscope. The time required for the first flower primordium to form was recorded. The development of floral buds was followed in detail from initiation until full development. In a preliminary study, the developmental progress of floral buds was found to be very similar to the scheme described by Ojehomon and his co-workers (1973). The floral stages were thus assigned according to the scheme shown in Fig. 2. By stage 10 all floral parts had differentiated. After this, bud length was used as the criterion of developmental progress. The length of small buds, where the corolla was still completely enclosed within the calyx, was measured from the base to the top of the calyx. Anthesis occurred 5 days after the corolla emerged beyond the calyx. The flowering date for the remaining plants was also recorded.

Field studies

In a tropical climate like Hawaii the daylength requirements of individual plants can be studied by planting them all under long day

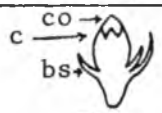
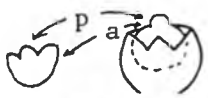
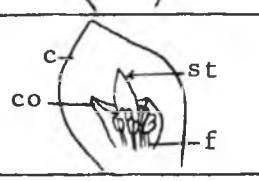
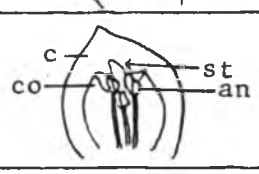
Stage		
1		First flower primordium (triad primordium) is initiated
2		First flower primordium gives rise to two lateral flower primordia (f) each of which is subtended by a bract (b)
3		First lateral flower primordium forms a pair of bracteoles (bs)
4		Initials of calyx (c) and corolla (co) appear
5		Presumptive pistil (p) and androecium (a) are differentiated
6		Presumptive androecium breaks into concretions
7		Connectives appear in concretions, recognizable as 10 sessile anthers (an)
8		Anthers have short free filaments (f) and are recognizable as stamens Pistil is differentiated into ovary and a long straight style (st)
9		Filaments have elongated to the length of style
		Stigma (stg) is differentiated At this stage all floral parts have differentiated
11		Length of flower bud - 2 mm
12		4 mm
13		6 mm
14		Corolla emerges beyond the calyx

Fig. 2. Stages in floral bud development in Phaseolus vulgaris

conditions during the summer months and assuming that flowering will occur whenever the daylength has gotten short enough for initiation. Thus, it should be possible to measure the photoperiodic requirements of many individuals in segregating F_2 populations easily and accurately in the field.

The parental lines in Table 1 were crossed in as many combinations as possible in the greenhouse. Pollination was carried out according to the method described by Buishand (1956). Crosses were made only under short days when synchronization of flowering of all lines was possible.

Seeds of all F_1's and parental lines were then planted in the greenhouse and backcrosses were made. Seed set was low and there was a limited supply of some F_1 plants, so all possible combinations were not obtained. Selfed seeds were also harvested from the F_1 plants to produce the F_2 generation.

Seeds of the parental lines, F_1's, F_2's, and backcrosses were planted on August 14, 1974 at the Poamoho Experimental Farm, Oahu. The farm is at an elevation of 265 m, the soil type is Wahiawa Silty Clay (Tropeptic Eutrustox). The average maximum and minimum temperatures during the experiment were 29.1 C and 19.6 C, respectively. Rainfall during this period was 11.5 cm. The plants were watered as needed by furrow irrigation.

The seeds were planted in rows spaced 120 cm apart. Within a row the seeds were spaced 30 cm apart. A maximum of 100 seeds of each F_2 was planted, 8 seeds of each F_1, 18 seeds of each backcross, and 15 seeds of each parental line.

The date of flowering of each plant was recorded. The plants were planted when the daylength was 12.9 hours and decreasing. The day-neutral types should flower in the usual 30-40 days from planting and short day types should flower when their required daylength was reached. The number of days to first flower would be a relative indication of the daylength requirement. For convenience of analysis, the flowering data are expressed as number of days to flowering instead of the daylength requirement at which flowering occurred since several days in succession often have the same daylength.

RESULTS

Photoperiodic response of parental lines

The mean number of days to first flower for each parental line when grown under natural daylength in the greenhouse is presented in Table 3. When planted in November, January, and February, the lines flowered more or less simultaneously. All lines were in bloom within 40 days after planting. However, when planted in April, July, and August differential responses were observed.

OSU and HAR always bloomed within 40 days after planting. In contrast to this, the other lines took much longer to flower in the summer than in the winter. In addition, some lines took longer to flower than others. When planted in July and August most lines bloomed in mid September, but 002 and 006 did not flower until mid October. When planted on April 25, no line except OSU and HAR flowered by August and all were then discarded.

The qualitative nature of the daylength response was confirmed by the flowering responses under controlled daylength shown in Table 4. Within the different photoperiods in which the plants bloomed, there was no significant difference for each line in number of days to flowering. At each daylength the line either flowered in the normal time or not at all.

OSU and HAR flowered under all daylength which is a day-neutral response. No flowering occurred on 002 and 006 under either 12, 14, or 16 hour days which means that more than 12 hours of dark period are

Table 3. Days to first flower of the parental lines when grown under natural daylength

Line	Date of planting											
	1/11/73		2/4/73		7/18/73		8/20/73		11/19/72		4/25/72	
	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
002	36.1	1.4	36.5	1.3	96.4	2.4	62.3	1.7	36.7	0.7	-[a]	-
005	36.5	1.0	36.4	1.5	62.0	2.4	43.3	0.9	36.8	1.2	-	-
006	36.3	1.4	36.9	1.2	96.4	2.4	62.8	1.7	37.4	1.1	-	-
999	33.1	0.6	35.4	1.1	59.5	2.2	43.0	0.6	37.1	1.1	-	-
081	33.0	1.3	33.5	0.9	59.9	1.3	32.7	0.6	33.5	1.3	-	-
831	34.0	1.1	36.0	0.7	59.8	1.8	34.9	0.8	34.8	1.3	-	-
914	32.6	1.6	34.1	1.4	62.9	2.1	36.6	0.5	37.0	1.0	-	-
916	30.3	1.2	33.3	1.3	66.8	1.6	37.0	1.1	34.1	0.8	-	-
924	35.9	1.1	34.6	1.4	66.4	1.9	36.8	0.8	34.6	0.7	-	-
OSU	33.6	0.7	32.5	1.0	33.5	1.2	32.8	1.3	32.0	1.2	30.0	1.3
HAR	35.1	0.9	32.8	1.3	33.5	1.2	34.6	0.8	34.8	1.4	32.8	1.2

[a]Denotes no flowering up to 115 days.

Table 4. Days to first flower of the parental lines grown under controlled photoperiods of 8, 10, 12, 14, and 16 hours

Line	Photoperiod									
	8 hr		10 hr		12 hr		14 hr		16 hr	
	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
002	44.1	1.2	45.4	1.2	-[a]	-	-	-	-	-
005	43.0	0.7	43.8	0.8	44.4	0.6	-	-	-	-
006	45.0	0.5	44.6	1.1	-	-	-	-	-	-
999	43.1	0.6	43.4	0.8	44.6	0.8	-	-	-	-
081	40.6	0.9	40.4	0.7	40.1	0.7	-	-	-	-
831	42.0	0.9	43.0	0.8	43.3	0.8	-	-	-	-
914	39.6	1.0	40.4	1.0	42.6	1.3	-	-	-	-
916	40.8	1.6	42.9	1.2	41.3	0.7	-	-	-	-
924	44.3	0.6	42.3	1.0	44.0	0.9	-	-	-	-
OSU	31.0	0.9	30.9	0.7	32.1	0.7	33.0	1.4	34.8	1.2
HAR	33.9	0.8	33.0	0.8	32.9	1.0	34.1	0.4	34.6	1.3

[a]Denotes no flowering within 66 days.

needed for these lines to flower. Lines 005, 999, 081, 831, 914, 916, and 924 flowered under the 12-hour photoperiod but not under the 14- and 16-hour photoperiods which means that these lines have a critical dark period between 10-12 hours.

In the controlled daylength experiment, about 25 days were requied between the first inductive daylength and flowering. Therefore, it was assumed that the same interval occurred under natural daylength, and the inductive daylengths were inferred to occur about 25 days or less before the flowering date. On this basis, the inductive daylength for 002 and 006 was estimated to be a little less than 12 hours. The inductive daylength for 005, 999, 081, 831, 914, 916, and 924 was estimated to be 12.6 hours or less. Thus the results from both natural blooming and controlled daylength experiments agreed.

These results generally agreed with those of Hartmann (1969). Hartmann reported that 002, 006, and 916 flowered at daylengths between 11.5 and 11.8 hr, while 005, 999, 831, 081, 914, and 924 flowered at daylengths between 12.5 and 12.0 hours. The only difference found was that here 916 flowered under the 12 hour photoperiod. 002 and 006 were the latest to flower under the natural daylength, requiring a longer dark period than the other lines.

The P. vulgaris lines used in this study were therefore classified into three types according to their photoperiodic response in flowering (from Table 4):

Day-neutral	Intermediate (flower at 8, 10, 12 hour controlled photoperiods)	Sensitive (flower at only 8, 10 hour controlled photoperiods)
OSU	081	002
HAR	831	006
	914	
	916	
	924	
	999	
	005	

The three classes were clearly distinguishable when planted in field on August 14, 1974 (Appendix Table 16). However, there was a slight overlap between the day-neutral and intermediate classes.

Effects of temperature

The plants of line 924 were grown under 15 hour days to prevent floral initiation before they were transferred to the growth chambers with the two different temperature treatments. The 10-hour photoperiod in the growth chamber was inductive for floral initiation. Therefore, any difference in flowering date should indicate the effect of temperature on floral initiation and/or floral development.

The development of the first initiated buds was followed in detail. The first floral primordium is located at either the 6th, 7th, or 8th node. Under low temperature, only a slight delay in initiation of the floral primordium was found. After the plants were shifted to the short photoperiod, the first floral primordium could be seen in 9 days under the lower temperature and 8 days under the

higher temperature. Following initiation, the rate of development was also inhibited by the lower temperature. This inhibition at the lower temperature resulted in a 3 to 7 day delay in flowering (Table 5).

It was reported that in determinate varieties of P. vulgaris, floral initiation occurred within 2 weeks after planting when day-length is not a limiting factor (Kemp, 1973; Ojehomon, 1966, 1973; Wivutvongvana and Mack, 1974). Five to 7 days were required for a primordium to differentiate floral parts (Wivutvongvana and Mack, 1974). Ojehomon (1966) observed that the period required for the initiation of the floral primordium increased with a decrease of the temperature at which the plants were grown. When grown at a constant temperature of 25 C the first floral primordium initiated 5 days earlier than when grown at 20 C. No floral initiation was observed at 10 C or less. In contrast, in an indeterminate dry bean variety, Padda and Munger (1969) reported that floral initiation occurred under all photoperiods and temperature conditions but further development of the floral primordium was delayed or completely inhibited by long photoperiods.

In the present study, the delay in flowering caused by the low temperature treatment may be attributed to the low night temperature of 16.7 C.

In general, the temperature of the dark period is particularly important in determination of flowering (Vince-Prue, 1975). In contrast, day temperature of a wide range has relatively less effect. In Honolulu, the average minimum temperature, for the coldest month,

Table 5. Mean number of days in the development of the first initiated flower bud of plants grown in two different temperature treatments

Treatment	Treatment start to floral initiation	Time interval (number of days)		Seeding to flowering
		Floral initiation to stage 10	Stage 10 to stage 14	
Low temperature (24.4 C/16.7 C) (7 plants)	9	11	7	47.38 ± 0.92
High temperature (30.0 C/24.4 C) (8 plants)	8	9	5	42.14 ± 0.88

is 18.3 C and the average minimum temperature during the field experiment (August 14 - October 31, 1974) was 19.5 C. Moreover, the daily duration for the low temperature in nature will be shorter than the 14 hour (dark period) in the growth chamber in this study.

Thus, since all plants were subjected to the same night temperatures during the field experiment, and these temperatures were not low enough to severely delay flowering, it is assumed that temperature effects are insignificant on these populations.

Intercrosses within types

All plants of the day-neutral lines flowered within 38 days after planting (Appendix Table 16). The seven intermediate lines flowered between 38 and 56 days after planting. During this period, the daylength was decreasing from 12.2 to 11.8 hours. Plants of the sensitive lines started flowering 63 days after planting when the daylength was less than 11.7 hours. The range of flowering date for individual parents ranged from 6 to 10 days and the variances were small, ranging from 1.8 to 9.2 (Table 6) which indicates the parents were uniform.

The number of F_1 plants which were tested for their photoperiodic response was small, but all F_1 plants flowered within the range of their parents (Appendix Tables 18 and 19). The F_2 progenies also generally flowered within the range of their parents. The F_2 progenies of the two neutral parents were all day-neutral, starting to flower before inductive short days occurred. The F_2 progenies of the two sensitive parents were all sensitive, flowering after the daylength

Table 6. Days to first flower of parents and F_2's of crosses between parents with same phenotype (planted 8/14/74)

Parents	Mean	Range	Variance	F_2	Mean	Range	Variance
Day-neutral				Day-neutral			
OSU	32.3	28-35	6.0	OSU X HAR	33.3	29-38	5.7
HAR	35.3	32-38	3.0				
				Intermediate			
Intermediate				081 X 831	43.3	37-49	5.0
081	40.8	38-45	4.4	081 X 914	41.1	36-47	6.3
831	43.6	41-48	3.8	081 X 916	42.8	36-48	3.8
914	44.9	41-48	5.7	081 X 924	46.2	41-55	9.2
916	42.7	41-46	1.8	831 X 914	44.3	37-50	4.3
924	47.6	43-52	6.9	831 X 916	43.7	41-51	6.6
999	51.6	48-55	7.1	831 X 924	47.3	44-53	5.5
005	53.5	49-56	4.7	914 X 916	45.0	42-52	10.7
				914 X 924	48.7	42-56	11.9
Sensitive				916 X 924	47.2	43-54	11.6
002	66.2	63-69	3.2	924 X 005	49.5	44-54	4.5
006	67.8	64-73	9.2	916 X 999	49.5	43-56	13.4
				999 X 005	56.4	47-62	7.0
				Sensitive			
				002 X 006	68.7	61-76	10.0

had reached 11.7 hours and after all the intermediate parents had flowered. The F_2 progenies of the intermediate parents all flowered at intermediate daylengths (between 38 and 56 days after planting), with one exception, the cross of 005 X 999, in which many individuals flowered later than other intermediate types, even overlapping a little with the sensitive type. The range of flowering dates for individual F_2 populations ranged from 9 to 15 days and the variances were small (Table 6), although a little larger than the parents in some cases. It was thus concluded that the division of the parents into three classes on the basis of their flowering responses was further confirmed by their breeding behavior in crosses within the same type. It seems quite likely, however, that there are differences within the intermediate type, so that these parents do all have the same major genotype, but differ from each other by some minor genes.

Intercrosses between types

Neutral X Intermediate. The F_1 plants flowered between 38 and 46 days after planting, entirely within the range of the intermediate parents (38-56 days) (Appendix Table 20). The F_2 plants flowered between 26 and 56 days after planting. Many F_2 populations exhibited larger variances than the parents (Table 7). There seems to be two flowering peaks on the 36th and 43rd day, with more plants flowering at intermediate daylengths (Fig. 3). The possibility of explaining these results with a one gene 3:1 ratio was investigated. If all plants which flowered on the 38th day or earlier were classified as day-neutral and all plants which flowered on the 39th day and later

Table 7. Days to first flower of F_1 and F_2 of Neutral X Intermediate (planted 8/14/74)

Cross	F_1	F_2		
	Mean	Mean	Range	Variance
OSU X 081	41.5	39.1	28-46	15.9
OSU X 831	40.3	42.1	33-47	12.2
OSU X 916	41.0	41.4	32-49	11.0
OSU X 924	42.0	42.4	31-51	12.4
OSU X 999	43.0	43.2	29-56	33.9
HAR X 914	41.0	38.4	28-49	32.5
HAR X 916	39.8	38.9	26-48	35.4
HAR X 924	43.0	41.8	30-49	22.6
HAR X 999	41.5	42.9	28-55	22.6
HAR X 005	42.3	39.5	30-49	19.6

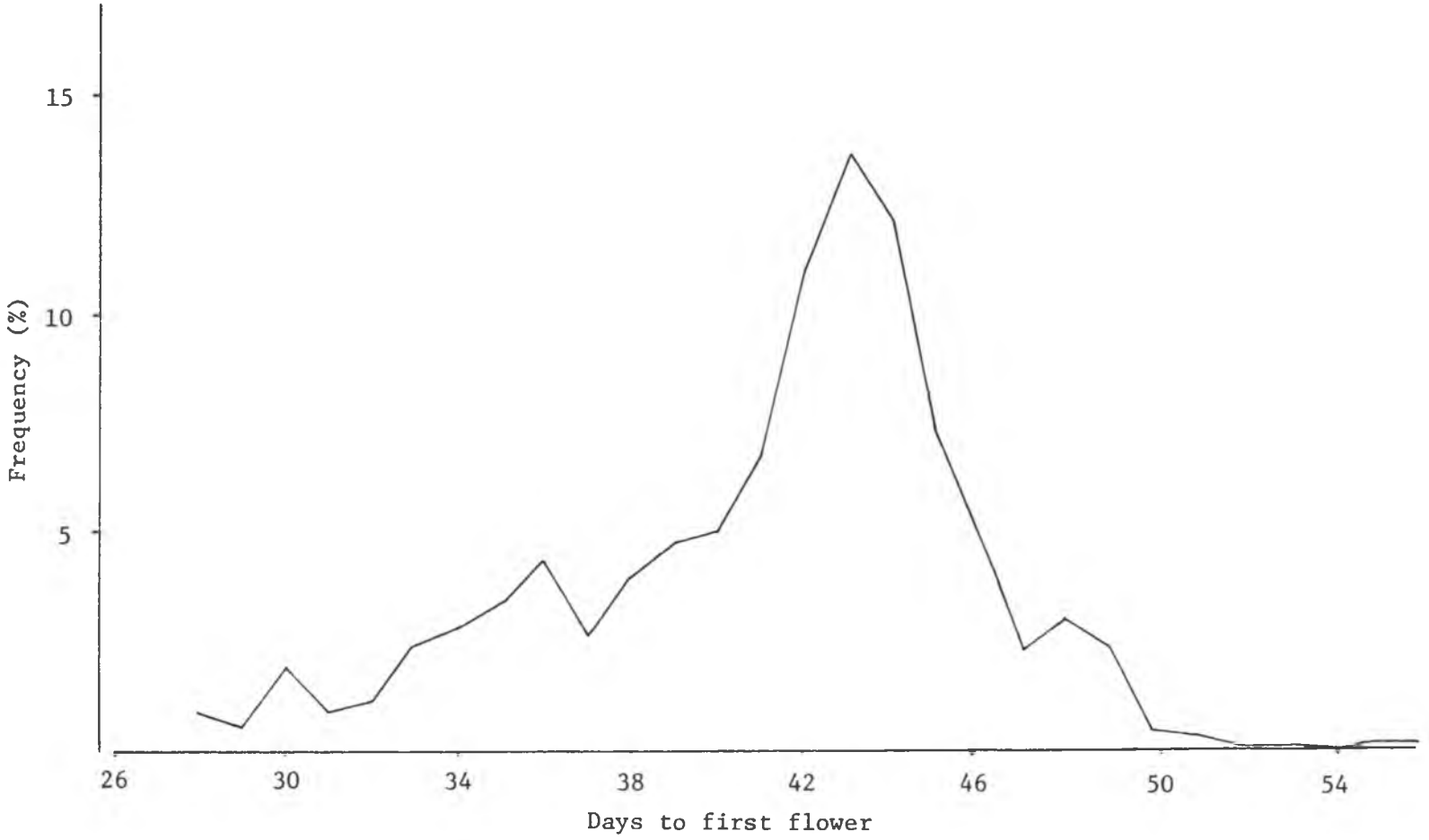


Fig. 3. Frequency distribution of days to first flower in F_2 between neutral and intermediate types (planted 8/14/74).

were classified as intermediate, the F_2 progenies in total segregated into 169 day-neutral to 502 intermediate, giving an almost exact fit to a 3:1 ratio with the intermediate type being dominant. It was tentatively concluded, therefore, that the day-neutral and intermediate types differ by one major gene, with the requirement for a short-daylength for flowering dominant to the lack of such a requirement.

In the backcrosses to intermediate parents, although the number of plants tested was limited, all plants were of the intermediate type. In the backcrosses to day-neutral parents, the plants segregated into 28 day-neutral and 16 intermediate, giving an acceptable fit to a 1:1 ratio. These backcross results agree with the one dominant gene hypothesis.

Intermediate X Sensitive. All the F_1 plants flowered between 48 59 days after planting, mostly within the range of the intermediate parents (38 to 56 days) (Appendix Table 21), but all earlier than the sensitive parents (63 to 73 days). In the F_2 populations more plants flowered like intermediate parents than like the sensitive ones. All of the F_2 populations, except 999 X 002 and 999 X 006, exhibited higher variability than the parents (Table 8). Again, there appeared to be a biomodal distribution in the F_2, with a larger intermediate flowering group with a peak on the 53rd day and a smaller sensitive group with a peak on the 65th day (Fig. 4). The possibility of attributing these results to a one gene difference was tested. If all plants which flowered up to the 58th day after planting were classified as intermediate and all plants which flowered on the 59th day or later

Table 8. Days to first flower of F_1 and F_2 of Intermediate X Sensitive (planted 8/14/74)

Cross	F_1	F_2		
	Mean	Mean	Range	Variance
831 X 002	51.0	52.7	45-62	23.4
914 X 002	52.3	54.6	44-68	29.4
914 X 006		56.0	45-68	34.7
916 X 002	49.3	54.7	48-66	30.5
916 X 006	51.0	55.6	45-68	38.8
999 X 002	55.0	56.9	54-64	4.5
999 X 006	56.0	57.8	53-63	8.1
005 X 006	56.5	54.9	47-68	24.4

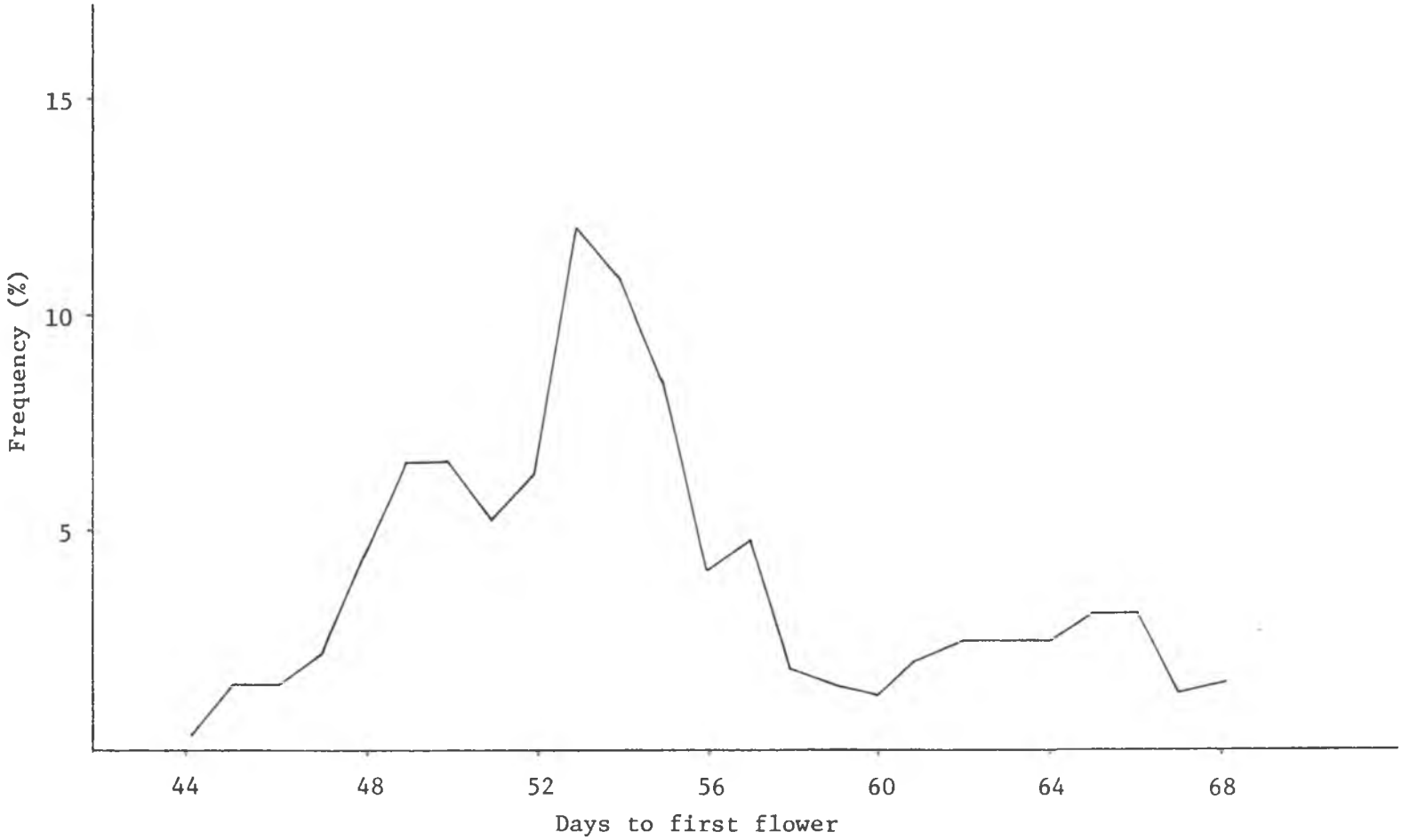


Fig. 4. Frequency distribution of days to first flower in F_2 between intermediate and sensitive types (planted 8/14/74).

were classified as sensitive, the F_2's (excluding 999 X 002 and 999 X 006) segregated into 244 intermediate to 69 sensitive, which is an acceptable fit to a 3:1 ratio. The tentative conclusion was therefore made that the intermediate and sensitive parents also differ by one major gene, with the requirement for a longer dark period being recessive.

The results obtained from 999 X 002 and 999 X 006 are difficult to explain. Although they show little variability with low variance and a much narrower range than other intermediate X sensitive F_2 populations, they do range over part of both of the intermediate and sensitive ranges and are somewhat bimodal in their distribution (Fig. 5). If they are divided into intermediate and sensitive like the other populations, they divided into 128 intermediate to 38 sensitive, which is quite an acceptable fit to a 3:1 ratio. Since 999 also gave unusual results when crossed with 005, another intermediate parent, it is concluded that 999 differs in genetic constitution from the other intermediate parents. Perhaps 999 also differs from the sensitive types by one major gene, but a different gene than is present in other intermediate lines.

In the backcrosses to intermediate parents all plants flowered at intermediate daylengths. The limited number of plants from backcrosses to sensitive parents flowered between 55 and 66 days after planting, with an acceptable fit to 1 intermediate : 1 sensitive ratio. These backcross results agree with the one dominant gene hypothesis again.

Neutral X Sensitive. In three crosses of neutral X sensitive, six plants of two F_1's flowered at 40-42 days and two plants of the

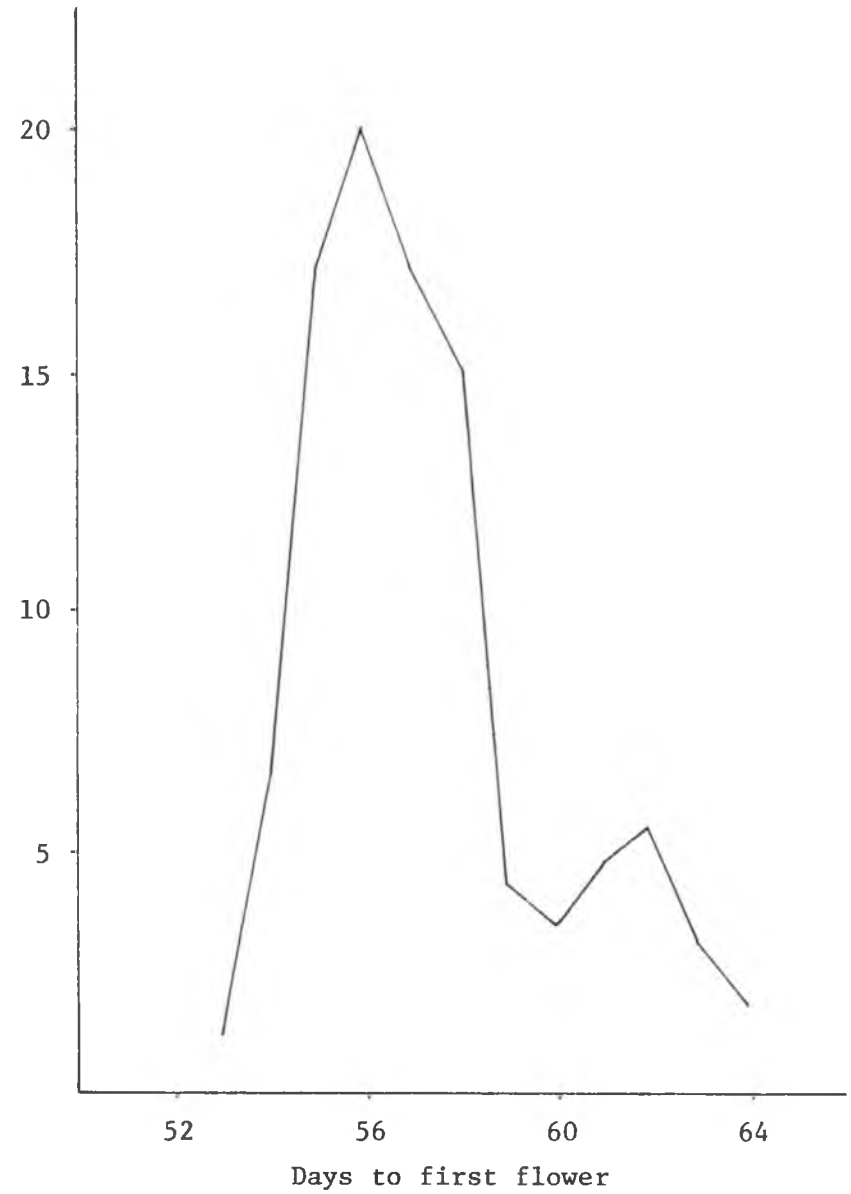


Fig. 5. Frequency distribution of days to first flower in F_2 between 999 and sensitive types (planted 8/14/74).

third flowered at 51 days after planting (Appendix Table 22). Two F_2 populations exhibited large variances and included both neutral and intermediate types (Table 9). The third F_2 (the one from the F_1 which flowered at 51 days) had a low variance and included only intermediate types. No sensitive types were observed. The number of backcross plants tested for the daylength response was limited. However, all the plants from backcrosses to sensitive parents flowered at intermediate daylength (between 48 and 55 days after planting), while some plants from backcrosses to neutral parents were day-neutral while others flowered at intermediate daylengths. No simple explanation for these results was apparent.

Table 9. Days to first flower of F_1 and F_2 of Neutral X Sensitive (planted 8/14/74)

Cross	F_1	F_2		
	Mean	Mean	Range	Variance
OSU X 002	51.0	49.1	42-56	11.5
HAR X 006	40.7	40.4	31-56	23.5
HAR X 002		44.6	34-56	46.5

DISCUSSION AND CONCLUSIONS

When the day-neutral and intermediate types were crossed, the F_1's flowered at the same time as the intermediate parents. When the F_2 plants which flowered on the 38th day or earlier were classified as neutral and those which flowered on the 39th day or later were classified as intermediate, an almost exact fit to a ratio of 1 neutral:3 intermediate was observed, suggesting a one-gene difference with the intermediate type being dominant. When the intermediate and sensitive types were crossed, the F_1's also flowered at the same time as the intermediate parents. When the F_2 plants which flowered on the 58th day or earlier were classified as intermediate and those which flowered on the 59th day or later were classified as sensitive, a good fit to a ratio of 3 intermediate:1 sensitive was observed, again suggesting a one-gene difference but this time with the intermediate type dominant to the sensitive type. When the day-neutral and sensitive types were crossed, the F_1's again flowered at the same time as the intermediate types. However, in three F_2 populations, the ratios found were: all intermediate; 2 neutral:13 intermediate; and 20 neutral:33 intermediate.

Thus, the intermediate type seems to be dominant to both the neutral and sensitive types and to differ from them by very few major genes, since many parental types were recovered in the F_2 and the distribution was bimodal with two major classes. However, when the extremes (day-neutral and sensitive) were crossed, most of the F_2 were intermediate, with some neutral types but no sensitive ones.

Possible genetic explanations for these results were considered. A one-locus hypothesis was rejected, because the F_2 between neutral and sensitive did not segregate into either 3:1 or 1:2:1. If there were two loci involved, then the F_2 between day-neutral and sensitive types should give a phenotypic ratio of 9 intermediate:3 neutral:3 sensitive:1 undetermined. This possibility was not accepted because no sensitive types were found and the ratio of intermediate:neutral was about 5:1, rather than the 3:1 (or less) indicated.

The next scheme considered was a system with the F_2's segregating in a 13:3 ratio instead of 3:1 since the two ratios are very similar. This hypothesis would propose the presence of some sort of inhibitor genes. Therefore, a model with four separate gene loci with dominance, epistasis, and independent segregation was hypothesized. The following assumptions were made:

1. The completely recessive genotype conveys a moderately short daylength requirement for flowering (called intermediate here)
2. A dominant genes, N, overcomes this requirement and permits flowering at any daylength (called neutral here)
3. A dominant gene, I_N, inhibits the action of the N gene
4. A dominant gene, Q, intensifies the short daylength requirement (called sensitive here)
5. A dominant gene, I_Q, inhibits the action of the Q gene
6. The N gene is epistatic to the Q gene, so that when both are present, the phenotype is neutral.

The genotype of the day-neutral parents is then postulated to be N N i_n i_n q q I_Q I_Q, the genotype for the intermediate parents is postulated to be n n I_N I_N q q I_Q I_Q, and the genotype for the sensitive parent is postulated to be n n I_N I_N Q Q i_q i_q.

Thus, the day-neutral and intermediate parents differ at the N and I_N loci, with a 13 intermediate (n n I_N -, N - I_N -, and n n i_n i_n):3 neutral (N - i_n i_n) ratio expected in the F_2. The F_2 data which gave an almost exact fit to a 3:1 ratio was therefore tested to see if they could fit a 13:3 ratio (Table 10). The fit to the 13:3 ratio was not as good as to the 3:1 ratio for the pooled F_2. However, six of the individual F_2 populations fit a 13:3 ratio as compared to only four which fit a 3:1 ratio. A much better fit to a 13:3 ratio was obtained by changing those plants which bloomed on day 38 (the last day a neutral parent plant bloomed and the first day an intermediate parent plant bloomed, see Appendix Table 16) from the neutral to the intermediate class. Now not only the pooled F_2 data but also all the individual F_2 populations except HAR X 914, show an acceptable fit to a 13:3 ratio. The backcrosses, as shown, would give the same result in either case, so confirm either hypothesis, giving a 1:1 ratio with the neutral parents and 1:0 with the intermediate parents. A heterogeneity test excluding HAR X 914 indicates that the rest of the F_2 populations are from a homogenous population (Table 11).

The intermediate and sensitive parents are hypothesized to differ at the Q and I_Q loci, and would be expected to give a 13 intermediate (q q I_Q -,Q - I_Q -, and q q i_q i_q):3 sensitive (Q - i_q i_q)

Table 10. Segregation for days to first flower in progenies between neutral and intermediate parents (planted 8/14/74)

Cross	Classification		Chi-square		Classification		Chi-square
	Neutral (26-38 days)	Intermediate (39-56 days)	1:3 ratio	3:13 ratio	Neutral (26-37 days)	Intermediate (38-56 days)	3:13 ratio
F_2:							
OSU X 081	31	57	4.91*	15.68***	22	66	2.26
OSU X 831	6	37	2.80	0.65	6	37	0.65
OSU X 916	20	69	0.30	0.81	14	75	0.53
OSU X 924	13	87	7.68**	2.17	12	88	2.99
OSU X 999	9	57	4.55*	1.33	9	57	1.33
HAR X 914	34	31	25.85***	48.05***	31	34	36.66***
HAR X 916	9	16	1.61	4.88*	8	17	2.88
HAR X 924	20	58	0.02	2.43	17	61	0.48
HAR X 999	10	62	4.74*	1.12	10	62	1.12
HAR X 005	17	28	3.92*	10.70**	13	32	3.04
Pooled F_2	169	502	0.01	17.94***	142	529	2.56
Pooled BC_1					28	16 (1:1)	2.75
Pooled BC_2						21	

*significant at 5% level, **significant at 1% level, ***significant at 0.1% level

Table 11. Summary of data for 9 F_2 populations (excluding HAR X 914) based on 3:13 ratio

	d.f.	Chi-square
Total	9	15.28 ns
Pooled (111 vs. 495)	1	0.07 ns
Heterogeneity	8	15.21 ns

ns = not significant

ratio in the F_2. The F_2 data (not including the two crosses with 999) give an acceptable fit to either a 13:3 or a 3:1 ratio (Table 12). However, a better fit to a 13:3 ratio was obtained by changing those plants which flowered on day 59 from the sensitive to the intermediate class. All but one F_2 population now gives a good individual fit to the expected 13:3 ratio. The heterogeneity chi-square justified pooling of these data (Table 13).

Crosses between the neutral and sensitive parents would differ at all four loci and are hypothesized to segregate into 48 neutral:169 intermediate:39 sensitive in the F_2 (Table 14). No sensitive types were found in the present study, but the data were tested by pooling the expected intermediate and sensitive types together as one class. The F_2's segregated into 20 neutral to 121 intermediate, giving an acceptable fit to the expected 48:208 ratio (Table 15).

In summary, then, the neutral parents are postulated to have a dominant N gene permitting flowering at any daylength while both the intermediate and sensitive parents have the recessive n gene and the inhibitor of the N gene, I_N. The sensitive parents have a dominant Q gene which intensifies the short daylength requirement while both the neutral and intermediate parents have the recessive q gene and the inhibitor of the Q gene, I_Q. Two genes (at the N and I_N loci) therefore differentiate between the neutral and intermediate parents, another two genes (at the Q and I_Q loci) differentiate between the intermediate and sensitive parents, and a total of four genes differentiate between the neutral and sensitive parents. Although the

Table 12. Segregation for days to first flower in progenies between intermediate and sensitive parents (planted 8/14/74)

Cross	Classification		Chi-square		Classification		Chi-square
	Intermediate (44-58 days)	Sensitive (59-68 days)	3:1 ratio	13:3 ratio	Intermediate (44-59 days)	Sensitive (60-68 days)	13:3 ratio
F_2:							
831 X 002	44	9	1.82	0.11	45	8	0.47
914 X 002	38	9	0.86	0.00	40	7	0.46
914 X 006	33	12	0.07	1.85	33	12	1.85
916 X 002	44	12	0.38	0.26	45	11	0.03
916 X 006	47	21	1.25	6.57*	48	20	5.07*
005 X 006	38	6	3.03	0.76	38	6	0.76
Pooled F_2	244	69	1.46	2.23	249	64	0.59
Pooled BC_1	48						
Pooled BC_2					4	8 (1:1)	0.75

*significant at 5% level

Table 13. Summary of data for 6 F_2 populations based on 13:3 ratio

	d.f.	Chi-square
Total	6	8.63 ns
Pooled	1	0.59 ns
Heterogeneity	5	8.04 ns

ns = not significant

Table 14. Expected genotypes and phenotypes for photoperiodic response in progenies of crosses between neutral and sensitive types

Genotype	Phenotype	Frequency
N - I_N - Q - I_Q -	intermediate	81/256
N - I_N - Q - i_q i_q	sensitive	27/256
N - I_N - q q I_Q -	intermediate	27/256
N - i_n - Q - I_Q -	neutral	27/256
n n I_N - Q - I_Q -	intermediate	27/256
N - I_N - q q i_q i_q	intermediate	9/256
N - $i_n i_n$ Q - i_q i_q	neutral	9/256
N - $i_n i_n$ q q I_Q -	neutral	9/256
n n I_N - Q - i_q i_q	sensitive	9/256
n n I_N - q q I_Q -	intermediate	9/256
n n $i_n i_n$ Q - I_Q -	intermediate	9/256
N - $i_n i_n$ q q i_q i_q	neutral	3/256
n n I_N - q q i_q i_q	intermediate	3/256
n n $i_n i_n$ Q - i_q i_q	sensitive	3/256
n n $i_n i_n$ q q I_Q -	intermediate	3/256
n n $i_n i_n$ q q i_q i_q	intermediate	1/256

Table 15. Segregation for days to first flower in progenies between neutral and sensitive types (planted 8/14/74)

	Number of neutral plants	Number of intermediate plants	Number of sensitive plants	Chi-square (48:208)
Pooled F_2 (observed)	20	121	-	1.93
F_2 (expected on) 48:169:39	26.4	114.6		

population size of the F_2 between neutral and sensitive was not large enough to obtain conclusive evidence to verify this hypothesis, the scheme in terms of these four genes seems to satisfactorily explain the results obtained. There are, however, some aspects which are not readily explained in terms of these four genes. A wide range of flowering occurred within the intermediate parents, indicating additional genes with smaller effects may also be involved. Also, the different segregation in some crosses involving 999 suggests that this line may have a different genotype from the other intermediate types.

In agreement with earlier investigations (Coyne, 1967, 1970, 1972; Coyne and Mattson, 1964), the present study indicates that there are photoperiodic responses in beans controlled primarily by qualitative genes. However, the short-day varieties used in previous studies did not have a critical daylength requirement, flowering was delayed only under certain temperature regimes and long photoperiods, and thus they did not show the same kind of response as is reported here.

APPENDIX

(Tables 16-22)

Table 16. Days to first flower for individual plants of parental lines (planted 8/14/74)

Line	Days to flower																																									
	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	56	47	48	49	50	51	52	53	54	55	56-63	64	65	66	67	68	69	70	71	72	73
Day-neutral																																										
OSU (9)[a]	1		1	2		1	2	2																																		
HAR (14)					1	1	2	4	3	1	2																															
Intermediate																																										
081 (11)											1	1	5	1	1		1	1																								
831 (13)														2	1	4	3	1	1		1																				
914 (14)														1	1	4		2	2	1	3																				
916 (15)														1	8	3	1	1	1																						
924 (13)																1	1	1		4	1	2	1	1	1																
999 (8)																					1		3	1			1	2													
005 (10)																						1		1	1		3	3	1												
Sensitive																																									
002 (13)																													1	2	1	2	4	2	1						
006 (13)																														1	2	3	2	1		1	1		2		

[a]Numbers in parentheses denote number of plants.

Table 17. Days to first flower for individual plants of progenies between two day-neutral parents (planted 8/14/74)

Generation	Days to flower									
	29	30	31	32	33	34	35	36	37	38
F_2 (OSU X HAR) (20)[a]	1	1	4	1	5		4	3		1
(OSU X HAR) X OSU (4)			2	1	1					
(OSU X HAR) X HAR (1)										1

[a]Numbers in parentheses denote number of plants.

Table 18. Days to first flower for individual plants of progenies between two sensitive parents (planted 8/14/74)

Generation	Days to flower															
	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76
F_1 (002 X 006) (6)[a]				1			2	2	1							
F_2 (002 X 006) (68)	3	2		3	4	1	2	7	16	16	6	1	3	3		1

[a]Numbers in parentheses denote number of plants.

Table 19. Days to first flower for individual plants of progenies between intermediate parents (planted 8/14/74)

Generation	Days to flower																									
	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62
F_1:																											
081 X 831 (6)[a]						2	3		1																		
081 X 916 (4)					1		2			1																	
081 X 924 (8)							2	1	1	1	3																
081 X 005 (1)						1																					
831 X 914 (4)							1	2				1															
831 X 005 (1)									1																		
914 X 916 (4)									4																		
914 X 924 (4)								1			1	1			1												
914 X 005 (4)													3	1													
916 X 924 (5)										2	2					1											
916 X 999 (1)												1															
916 X 005 (1)									1																		
F_2:																											
081 X 831 (86)		2	1		2	7	18	22	14	13		1	3	3													
081 X 914 (75)	1	4	5	6	17	15	9	4	3	3	6	1															
081 X 916 (83)	2		4			1	19	36	14	4		1	2														
081 X 924 (71)						1	3	4	13	19	3	12	2	2	4	1	4	1	1	1							
831 X 914 (108)		2				3	16	15	23	17	23	2	6		1												
831 X 916 (55)						1	24	13	6	1			5	3	1	1											
831 X 924 (56)									7	8	3	13	12	5	4			4									
914 X 916 (85)							21	26	8	2	3	1	4	5	8	5	2										
914 X 924 (72)							2	5	4	5	3	5	8	5	14	6	6	3	3	2	1						
916 X 924 (40)								5	7	3	6	3	3	4	1	2	2	1	3								
916 X 999 (63)								5	4	4		2	12	9	1	4	3	8	5	4	2						
924 X 005 (29)									1		2	2	2	6	6	8		1	1								
999 X 005 (42)												1					1		4	10	10	4	3	3	4	1	1

Table 19. (Continued) Days to first flower for individual plants of progenies between intermediate parents (planted 8/14/74)

Generation	Days to flower																									
	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62
Backcrosses:																											
(081 X 831) X 081 (15)[a]		1	1	1			1	6	4	1																	
(081 X 831) X 831 (6)							1	2	2	1																	
(081 X 914) X 081 (1)								1																			
(081 X 916) X 081 (7)			1		2		2	1	1																		
(081 X 924) X 081 (2)					1						1																
(831 X 914) X 831 (3)										1	2																
(831 X 916) X 831 (4)									1	1	2																
(831 X 916) X 916 (4)								1	1	1	1																
(831 X 924) X 831 (6)										3	2	1															
(831 X 924) X 924 (13)							1	2			2	2	5		1												
(831 X 999) X 831 (4)										1		2	1														
(914 X 916) X 914 (12)								7	4	1																	
(914 X 916) X 916 (8)											8																
(914 X 924) X 914 (4)											3			1													
(914 X 924) X 924 (17)										1			2	4	5	1	2		1	1							
(914 X 005) X 914 (7)											6	1															
(914 X 005) X 005 (1)														1													
(916 X 924) X 924 (2)															2												
(916 X 005) X 916 (16)										1	13	1							1								
(916 X 999) X 916 (26)										1	14	10	1														
(924 X 005) X 924 (4)													3	1													

[a]Numbers in parentheses denote number of plants.

Table 20. Days to first flower for individual plants of progenies of Day-neutral X Intermediate (planted 8/14/74)

Generation	Days to flower																														
	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56
F_1:																															
OSU X 081 (4)[a]														1			2	1													
OSU X 831 (4)															3	1															
OSU X 916 (3)															1	1	1														
OSU X 924 (2)																	2														
OSU X 999 (3)																	1	1	1												
HAR X 914 (2)																2															
HAR X 916 (4)													2			1	1														
HAR X 924 (2)																	1		1												
HAR X 005 (4)													1				1	1			1										
HAR X 999 (6)															1	2	2	1													
F_2:																															
OSU X 081 (88)			2	1	3			2	3	6	5		9	9	11	10	9	11	5	1	1										
OSU X 831 (43)								2		1	2	1			3	9	3	6	2	7	6	1									
OSU X 916 (89)							1	2		3	4	4	6	5	2	3	10	28	13	4	1	2		1							
OSU X 924 (100)						1		1	1	1	3	5	1	2	3	9	20	15	17	9	2	3	3	2	1	1					
OSU X 999 (66)				1	1	2	2	1		1	1			5	5	2	10	3	1	2	3	3	13	6	2	1					1
HAR X 914 (65)			3	2	1	1	4	4	3	3	5	5	3	2	2	3	4	1	6	8	3		1	1							
HAR X 916 (25)	1				3	1		1	1			1	1		1	3	5	3	1	1	1		1								
HAR X 924 (78)					1	1		3	5	4	3		3		1	2	5	11	17	7	8	4	1	2							
HAR X 005 (45)					2		1		3	2	5		4	5	4	2	3		10	3				1							
HAR X 999 (72)			1		1				3	2	1	2		4	2	3	4	14	10	7	8	3	1	3			1	1		1	
Backcrosses:																															
(OSU X 999) X OSU (18)			1		1		1			5	2	1				1	1	1		1	3										
(HAR X 914) X HAR (4)			1			1				1								1													
(HAR X 916) X HAR (5)				1			1		1	1											1										
(HAR X 924) X HAR (2)										2																					
(HAR X 005) X HAR (5)							1		1	2						1															
(HAR X 999) X HAR (10)								2		1	1	1					1	4													
(HAR X 914) X 914 (8)																1	1	3	3												
(HAR X 916) X 916 (3)																1					2										
(HAR X 924) X 924 (8)																1	1	1	1			2	1		1						
(HAR X 005) X 005 (2)																		1		1											

[a]Numbers in parentheses denote number of plants.

Table 21. Days to first flower for individual plants of progenies of Intermediate X Sensitive (planted 8/14/74)

Generation	Days to flower																								
	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68
F_1:																									
831 X 002 (4)[a]							3				1														
831 X 006 (4)							1			2		1													
914 X 002 (3)							1		1			1													
916 X 002 (4)					1	2		1																	
916 X 006 (2)							1		1																
924 X 006 (7)							1				2		1	2		1									
005 X 006 (2)													1	1											
999 X 006 (1)													1												
999 X 002 (3)											1	1	1												
F_2:																									
831 X 002 (53)		1	4		5	6	5	6	3	3	1	5	2	2	1	1	2	3	3						
914 X 002 (47)	1	1	1		3	3		1	2	8	7	6	1	1	3	2	2				1	1	1	1	1
914 X 006 (45)		1		2		2	1	1	2	11	5	4		4						3	3	2	2	1	1
916 X 002 (56)					4	6	5	6	4	2	6	4	4	3		1			2	2	1	3	3		
916 X 006 (68)		2		1	1	4	8	3	9	3	7	4	2	2	1	1		4	2	2	2	3	3	2	2
005 X 006 (44)				4	1		2			11	8	4	4	3	1				1	1	1	1	1		1
999 X 002 (86)											5	18	22	14	15	2	3	2	3	1	1				
999 X 006 (80)										2	6	11	11	14	10	5	3	6	6	4	2				
Backcrosses:																									
(836 X 006) X 831 (5)	1		2	2																					
(914 X 002) X 914 (11)		1	4		3	3																			
(916 X 002) X 916 (2)						1	1																		
(916 X 006) X 916 (10)					2	3	1	2	1		1														
(924 X 006) X 924 (14)						1	1		4	2	1	2	1	2											
(999 X 002) X 999 (5)											1	3			1										
(999 X 006) X 999 (1)								1																	
(005 X 006) X 005 (3)												2	1												
(831 X 006) X 006 (1)												1													
(914 X 006) X 006 (1)																	1								
(916 X 006) X 006 (1)															1										
(916 X 002) X 002 (4)														1			1						2		
(924 X 006) X 006 (3)																	1		1	1					
(005 X 006) X 006 (2)												1										1			

[a]Numbers in parentheses denote number of plants.

Table 22. Days to first flower for individual plants of progenies of Day-neutral X Sensitive (planted 8/14/74)

Generation	Days to flower																												
	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56
F_1:																													
OSU X 002 (2)[a]																								2					
OSU X 006 (3)														1	2														
HAR X 006 (3)													1	2															
F_2:																													
OSU X 002 (73)															1	3	3	5	4	9	8	10	5	4	7	7	2	4	1
HAR X 002 (15)							2					2	1				3	1	2				1			1		1	1
HAR X 006 (53)				1		1	5	1	3	7	2		4	7	5	8	2		3	1	1					1			1
Backcrosses:																													
(OSU X 002) X 002 (3)																										1	1	1	
(HAR X 002) X 002 (3)																					1			2					
(OSU X 002) X OSU (2)												1						1											
(HAR X 002) X HAR (8)						2		1								2	1				1					1			

[a]Numbers in parentheses denote number of plants.

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